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Effect of harvest intensity on development of natural regeneration and shrubs in an Ontario boreal mixedwood stand

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Abstract

Resource managers in northern Ontario need guidelines for establishing productive species mixtures and maintaining a viable conifer component through natural regeneration on upland boreal mixedwood (BMW) sites. The hypothesis that partial cutting favours conifers by inhibiting development of hardwood reproduction and associated competitors was tested. Harvesting to nominal basal area (BA) reductions of 0, 36, 68, and 100% was conducted in a northeastern Ontario mixedwood stand dominated by trembling aspen (*Populus tremuloides* Michx.) in the overstory and balsam fir (*Abies balsamea* [L.] Mill.) and shrubs in the understory. A positive linear relationship existed between photosynthetically active radiation (PAR) transmittance and initial BA reduction at 1, 3, and 5 years after harvesting. However, the relationship weakened over the 4-year period. Although BA reduction level did not account for significant variation in height growth of conifer advance regeneration, it explained 31% of the variation in conifer sapling diameter growth, 61% of the variation in hardwood regeneration height growth, and 21% of the variation in shrub height growth. Based on post-harvest height comparisons among conifers, hardwoods, and shrubs, partial cutting to promote conifer advance regeneration on BMW sites cannot be recommended. Maintaining a viable understory of shade-tolerant conifers for the next rotation may be more feasible than promoting conifer–hardwood overstories in the current rotation. The increase in sapling growth with BA reduction level implies that the entire overstory should be removed if the site is adequately stocked with conifer saplings. Similarly, harvesting should remove the entire overstory if the objective is to maximize growth of hardwood regeneration. Clearcutting promoted growth of both hardwood crop trees and shrubs, but hardwoods remained dominant after 5 years. Height development patterns indicate that regeneration and competitors should be monitored long enough following harvesting to determine whether additional interventions may be necessary to achieve stand structure objectives. Further studies are required to investigate the effects of other factors on advance regeneration, such as pattern and season of harvest and degree of soil disturbance.
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Keywords: *Abies*; Clearcutting; Competition; Diameter; Height; Mixedwood management; Partial cutting; *Picea*; *Populus*; Transmittance

1. Introduction

Forest resource managers are increasingly interested in mixed-species stands as the benefits of these stand types become more widely understood. Promoting species mixtures may improve habitat diversity, pest resistance, soil nutrient status, viewscape appeal, species utilization, and regeneration costs (MacDonald, 1995). Furthermore, stands of perennial plants with a diversity of species can outproduce monocultures of the best-producing single species (Tilman et al., 2001). Growing stratified mixtures of species is

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advisable on productive sites where hardwoods grow well and successional tendencies make vegetation difficult to control (Smith et al., 1997). However, silvicultural practices on mixedwood sites often foster successive rotations of similar stand composition, decreasing diversity and opposing the natural pattern of species replacement (Bergeron and Harvey, 1997).

Boreal mixedwood (BMW) sites in Ontario often become dominated by hardwoods and undesirable conifer species following harvesting (Yang and Fry, 1981; Hearnden et al., 1992). Thus, resource managers need reliable guidelines for achieving desirable mixtures of crop species. Weeding is required after partial cutting or clearcutting to ensure success of artificially regenerated conifers in BMW stands (MacDonald and Thompson, 2003). Well-established conifer advance regeneration may survive and grow well without weeding after partial cutting, but this approach has not been tested in Ontario BMW stands. Alternative methods such as partial cutting are needed for maintaining conifers on competitive sites because herbicides may reduce plant diversity (Newmaster et al., 1999) and the public opposes herbicide use in forestry (Lautenschlager et al., 1998).

Harvesting to protect advance regeneration has gained considerable interest across North America (Ruel et al., 2000). The response of advance regeneration may be more important than new seedling recruitment following various levels of canopy opening (Kneeshaw et al., 1998) and relying on advance regeneration is more cost-effective than planting for achieving full or partial conifer stocking in BMW stands (Greene et al., 2002). More work is necessary to understand the long-term effect of small-scale canopy openings on understory growth in BMW stands.

Trembling aspen (*Populus tremuloides* Michx.) root systems may produce dense sucker regeneration when post-harvest soil temperatures reach 12–23 °C (Perala, 1990; Fraser et al., 2002), and parent root carbohydrate reserves promote rapid sucker growth (Perala, 1990). Partial cutting may restrict this growth advantage by providing residual overstories to limit increases in soil temperature. Residual overstories have been shown to inhibit development of competitive understory hardwoods in mixed-species stands (Andersson, 1985; Lieffers et al., 1999).

We hypothesized that partial cutting creates an environment that favours development of conifer advance regeneration, residual conifer saplings, and aspen suckers, while clearcutting promotes aspen and shade-intolerant shrubs at the expense of conifers. Since hardwood regeneration is usually prolific on harvested BMW sites, the main objective of this study was to assess the effectiveness of partial cutting for enhancing conifer growth.

2. Methods

The study was located in an aspen-dominated BMW stand east of Cochrane, Ontario (49°04′N, 80°26′W). The lacustrine-origin soils were fresh to moist and fine-textured. Prior to harvesting, gross total volumes of hardwoods and conifers were 302 and 93 $m^3\ ha^{-1}$, respectively. Understory vegetation was predominantly balsam fir (*Abies balsamea* [L.] Mill.), black spruce (*Picea mariana* [Mill.] B.S.P.), and hardwood shrubs such as speckled alder (*Alnus rugosa* [DuRoi] Spreng.), mountain maple (*Acer spicatum* Lam.), and beaked hazel (*Corylus cornuta* Marsh.). Pre-harvest stand characteristics are summarized in Table 1.

The randomized complete block experimental design included four harvesting treatments, each applied with careful logging around advance regeneration. Treatments were intended to remove 0, 36, 68, and 100% of the merchantable overstory basal area (BA), based on trees equal to or greater than 10 cm diameter at breast height (DBH), and were randomly assigned to four 100 m × 100 m plots within each of four replications. Overstory BA reductions of 20 and 60% in five 16-m wide leave strips would produce the correct overall BA reductions of 36 and 68%, respectively, when combined with clearcutting the intervening four 5-m wide travel corridors. However, stand structure made it difficult to obtain the planned BA reductions on all plots. For example, the 68% reduction was not attained because small trees close to travel corridors were substituted for large aspen that had been marked for removal but exceeded the reach or capacity of the cutting head. Residual overstories are compared among treatments in Table 2.

The plots were full-tree logged with a feller-buncher and a grapple skidder during January and February 1995. The cutting head was extended halfway into the

Table 1
Average pre-harvest stand characteristics across all treatment plots

Species	Overstory[a] age (years)		Overstory[a] height (m)		Overstory[a] BA (m^2 ha^{-1})		Regeneration density (stems ha^{-1})	
	Mean	S.D.[b]	Mean	S.D.	Mean	S.D.	Mean	S.D.
Balsam fir	60.46	10.76	12.48	1.69	0.89	0.55	3554.7	2925.1
Black spruce	72.34	7.30	13.75	0.49	5.26	2.67	208.3	331.6
White spruce	71.13	11.21	14.98	1.88	1.16	0.76	13.0	52.1
Jack pine	75.28	7.82	23.03	1.86	2.50	4.94	0.0	0.0
Trembling aspen	72.81	8.00	22.83	1.59	25.80	5.81	481.8	479.4
White birch	43.25	21.87	11.33	6.13	0.06	0.15	247.4	989.6
Other	–	–	17.74	3.06	0.05	0.10	26.0	104.2
All species	69.83	11.57	19.13	1.20	35.71	3.34	4531.3	3190.1

[a] Living trees ≥10.0 cm DBH.
[b] Standard deviation.

harvest strips from travel corridors on each side. Large aspen and balsam fir were harvested first, with black spruce and white spruce (*Picea glauca* [Moench] Voss) cut only if necessary to achieve the required BA reductions. Some overstory trees remained in clearcut plots after treatment because they were unmerchantable or could not be removed without damaging advance regeneration. Harvesting was designed to distribute residual overstory canopies as uniformly as possible in partially cut plots.

Each harvested plot contained a central circular overstory assessment plot with a radius of 25 m (0.2 ha), divided into 12 equal sectors or subplots. Twelve 2 m × 2 m understory assessment plots, equally spaced on the circumference of each circular plot to prevent trampling during overstory assessment, were used to measure regeneration and shrubs. Plot quadrants were each delineated as three adjacent sectors and their associated understory assessment plots.

The height and density of regeneration (trees less than 4.0 m tall), height and ground cover of shrubs, and DBH of saplings (trees equal to or greater than 4.0 m tall and 1.0–9.9 cm DBH) were recorded each summer from 1994 (the year prior to harvesting) to 1999, with the exception of 1998. All variables were averaged by plot quadrant.

Residual stands in the study area were partially defoliated by forest tent caterpillar (*Malacosoma disstria* Hübner) after harvesting. Infestation peaked on all plots in 1998, with hardwood defoliation averaging 60% on overstory assessment plots and 85% on understory plots. Hardwood regeneration recovered full crowns within 1–2 years.

Light level strongly influences regeneration performance in boreal stands (Lieffers et al., 1999). Thus, light was measured at 1.3 m above ground in a systematic sampling grid of 72 locations (approximately 5 m spacing) in each overstory assessment plot. A single measurement was obtained at each location

Table 2
Comparison of residual overstories 1 year after harvesting

Planned BA[a] reduction (%)	Actual BA[a] reduction (%)		Residual BA[a] (m^2 ha^{-1})		DBH (cm)		Hardwood BA[a] (%)	
	Mean	S.D.[b]	Mean	S.D.	Mean	S.D.	Mean	S.D.
0	−0.47	3.03	34.62	5.24	21.63	3.51	69.36	22.86
36	38.97	7.12	22.36	2.20	21.66	1.70	66.02	23.89
68	46.00	7.09	18.21	0.90	21.06	1.62	67.55	11.44
100	96.24	2.70	1.42	1.03	15.33	2.94	38.57	36.83

[a] BA of residual trees ≥10 cm DBH.
[b] Standard deviation.

between late June and late August each year. Photon flux density was measured in steps of 2 nm with a portable LI-1800 spectroradiometer (LI-COR Inc., Lincoln, NE), which uses an integral cosine receptor with 180° field of view. Transmittance was calculated by dividing PAR (400–700 nm) at each location by PAR in the open, and expressing the result as a percentage. Only PAR measurements between 11:00 and 15:00 EDST on sunny days were used in these calculations. Transmittance values were averaged for each plot quadrant.

Linear regression was used to compare the transmittance–BA reduction relationship among years since harvest, using the following model:

$$Y_i = \beta_0 + \beta_1 X_i + \varepsilon_i \quad (1)$$

where Y_i is the quadrant mean transmittance (1, 3, or 5 years after harvesting) and X_i the corresponding BA reduction. Regression lines were compared to evaluate the persistence of the initial treatment effect over time.

Since planned BA reduction treatments were not always achieved (Table 2), linear regression was more appropriate than analysis of variance for testing the effect of BA reduction on growth responses. Using quadrant means, each response variable was regressed against actual percent BA reduction using model 1, where Y_i is the response variable and X_i the corresponding percent BA reduction.

Response variables included 4-year (1995–1999) change in conifer advance regeneration height, conifer sapling DBH, hardwood regeneration height, and shrub height. Seedlings established during the 4-year assessment period were omitted in these growth response regressions. Advance regeneration windthrown during that period was also omitted because loss of a single large conifer in an understory assessment plot could greatly reduce mean height, obscuring the effect of BA reduction on growth of surviving advance regeneration. To avoid the effect of logging disturbance on survival and growth of advance regeneration and shrubs, the first year after harvesting (1995), rather than the year prior to harvesting, was used as the reference point for changes in all variables.

Height trajectories were determined from 1995 to 1999 for partially cut and clearcut plots, using the following polynomial model:

$$Y_i = \beta_0 + \beta_1 X_i + \beta_2 X_i^2 + \varepsilon_i \quad (2)$$

where Y_i is the mean height of conifer advance regeneration, hardwood regeneration, or shrubs, and X_i the year. Graphs of the polynomial fits were used to compare development of conifers, hardwoods, and shrubs during the 5 years after harvesting. Frequency distributions of conifer advance regeneration height in 1995 and 1999 were constructed for uncut, partially cut, and clearcut plots to compare changes in understory structure among harvesting treatments. For analyses of height development, the partial cut treatment was based on plots with nominal BA reductions of 36 and 68%.

Since the data used for analysing the effect of BA reduction on transmittance and growth adequately conformed to the assumptions of linear regression models, transformations were not required. SAS® 8.02 (SAS Institute Inc., Cary, NC) was used for growth response analyses, and Statistica® 6.0 (StatSoft Inc., Tulsa, OK) was used for transmittance analyses and all graphics.

3. Results

3.1. Light relationships

Significant linear relationships existed between light transmittance and initial BA reduction at 1, 3, and 5 years after harvesting (Fig. 1). However, the regression coefficient and adjusted r^2 declined over the 4-year period. At 100% BA reduction, mean transmittance fell from 50% after 1 year to 37 and 27% after 3 and 5 years, respectively (Fig. 1). Even at 50% BA reduction, transmittance fell from 31% after 1 year to 26 and 22% after 3 and 5 years, respectively.

3.2. Growth responses

Five years after harvesting, mean values of sapling DBH, hardwood and shrub height, hardwood density, and shrub ground cover increased with BA reduction level, but mean height of conifer advance regeneration was lowest in the partial cut treatment (Tables 3–5). Mean height of conifer advance regeneration was less than that of hardwoods in the partial cut and clearcut treatments and less than that of shrubs in all treatments. Variation in mean height was greater for conifers than for hardwoods.

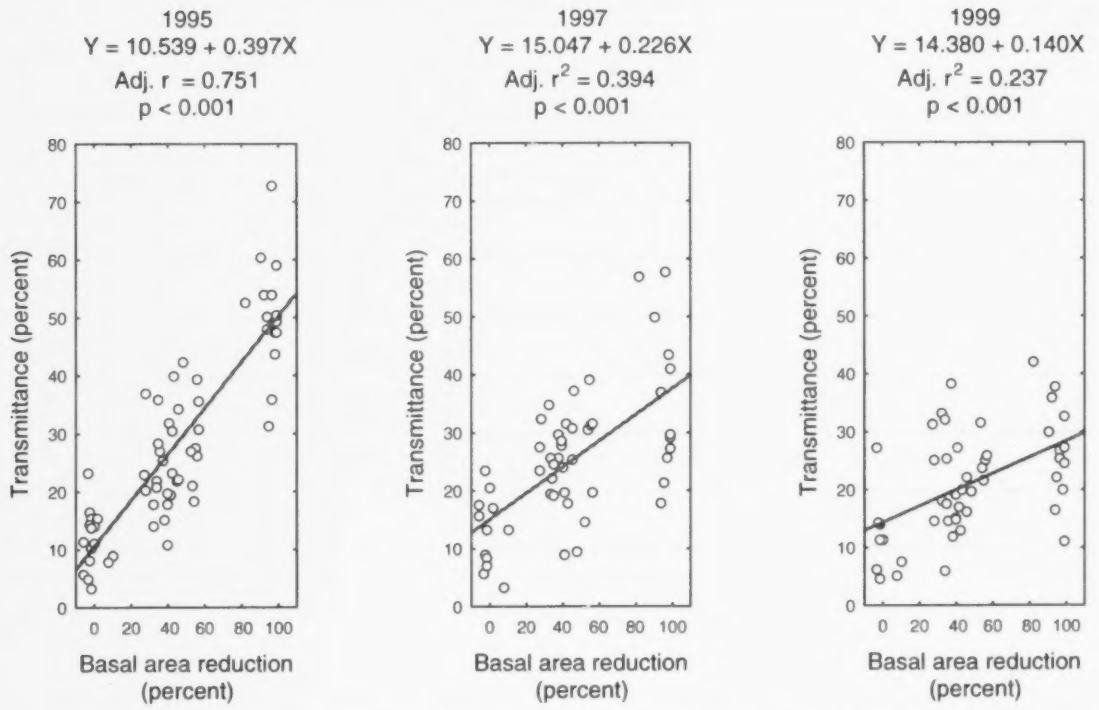

Fig. 1. Relationship between percent transmittance at 1.3 m above ground and BA reduction in 1995, 1997, and 1999 (1, 3, and 5 years after harvesting, respectively).

Four-year height growth of conifer advance regeneration was not linearly related to BA reduction, and no non-linear patterns were evident in plots of residual errors. However, 4-year DBH growth of residual conifer saplings was positively related to BA reduction (adjusted $r^2 = 0.312, P < 0.001$), with mean DBH

Table 3
Status of conifer crop trees in 1999, 5 years after harvesting

Treatment	Advance regeneration[a] height (cm)		Sapling[b] DBH (cm)	
	Mean	S.D.[c]	Mean	S.D.
Uncut	101.58	93.35	5.74	2.33
Partial cut	71.14	78.42	5.88	2.17
Clearcut	139.78	133.90	6.23	2.49

[a] Trees <4.0 m tall.
[b] Trees ≥4.0 m tall and 1.0–9.9 cm DBH.
[c] Standard deviation.

Table 4
Status of hardwood regeneration in 1999, 5 years after harvesting

Treatment	Height (cm)		Density (stems ha^{-1})	
	Mean	S.D.[a]	Mean	S.D.
Uncut	59.12	31.67	5417	5018
Partial cut	100.89	62.93	9661	4578
Clearcut	177.27	70.81	17292	7481

[a] Standard deviation.

Table 5
Status of shrub competition in 1999, 5 years after harvesting

Treatment	Height (cm)		Ground cover (%)	
	Mean	S.D.[a]	Mean	S.D.
Uncut	109.01	84.02	33.44	23.99
Partial cut	129.79	87.70	41.10	21.17
Clearcut	168.04	87.73	51.04	25.78

[a] Standard deviation.

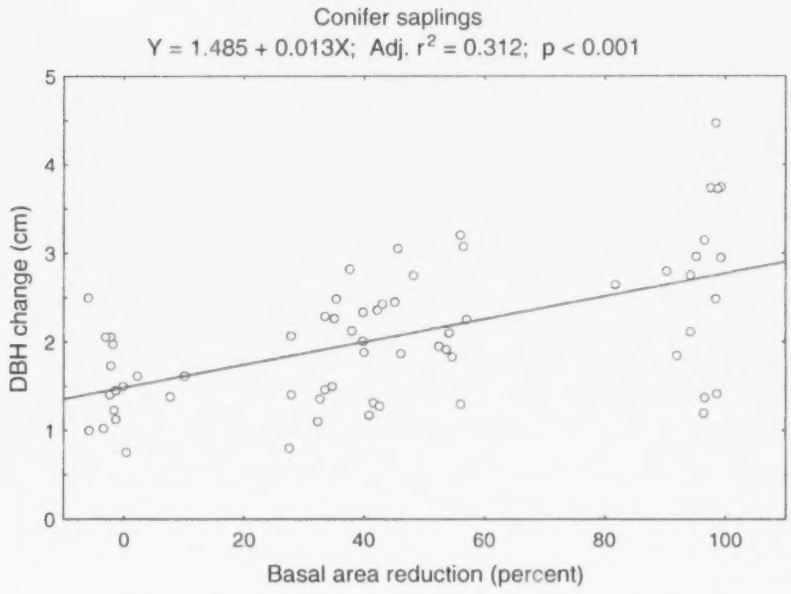

Fig. 2. Relationship between 4-year change in mean DBH of conifer saplings and initial BA reduction.

growth in the clearcut treatment nearly double that in the uncut treatment (Fig. 2).

Four-year height growth was positively related to BA reduction for both hardwood regeneration (adjusted $r^2 = 0.610, P < 0.001$) (Fig. 3) and shrubs (adjusted $r^2 = 0.207$, $P < 0.001$) (Fig. 4). Height growth of shrubs was less than that of hardwoods at all BA reduction levels.

3.3. Height trajectories

Initially, mean height of conifer advance regeneration exceeded that of hardwood regeneration (Figs. 5 and 6) because of the height advantage of pre-established conifers. However, mean height of hardwoods surpassed that of conifers within 2 years in partially cut plots and 3 years in clearcut plots. Mean height of shrubs exceeded that of conifer and hardwood regeneration for the first 5 years in the partial cut treatment (Fig. 5), but hardwoods surpassed shrubs by the fourth year in the clearcut (Fig. 6). Mean height of conifers, hardwoods, and shrubs peaked earlier in the partial cut than in the clearcut.

3.4. Conifer height distributions

Frequency distributions of conifer advance regeneration height the first year (1995) and fifth year (1999) after harvesting are presented for the uncut, partial cut, and clearcut treatments in Figs. 7–9, respectively. Heights were characterized by large variations around mean values, but distribution patterns were similar in 1995 and 1999 within each treatment. Over the 4-year period, a net shift in density occurred from the 50 cm class into the 150 and 250 cm classes in the uncut treatment and from the 250 cm class into the 350 cm class in the partial cut and clearcut treatments. In both 1995 and 1999, densities in the 50 and 150 cm classes were lower in the clearcut than in the partial cut.

4. Discussion

4.1. Light relationships

An important mixedwood management challenge is to determine the level of BA reduction (enhancement

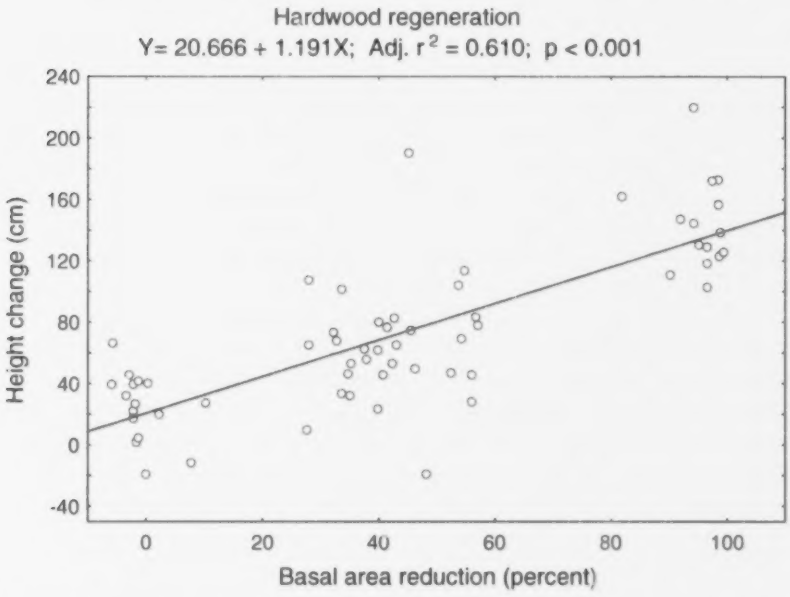

Fig. 3. Relationship between 4-year change in mean height of hardwood regeneration and initial BA reduction.

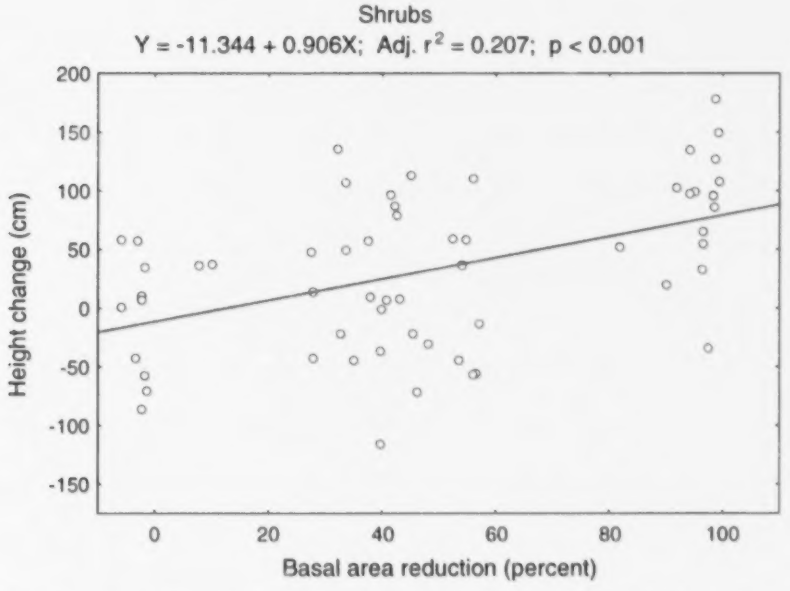

Fig. 4. Relationship between 4-year change in mean height of shrubs and initial BA reduction.

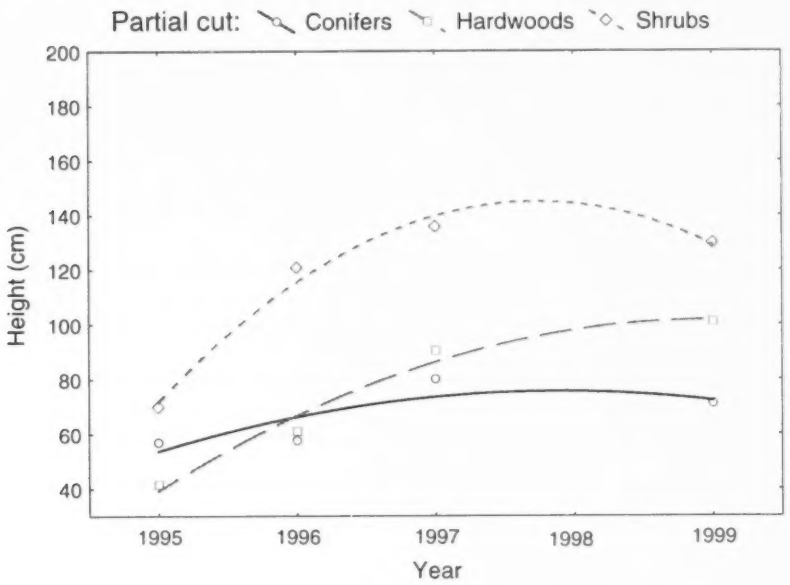

Fig. 5. Mean height trajectories of conifer advance regeneration, hardwood regeneration, and shrubs during the first 5 years after partial cutting.

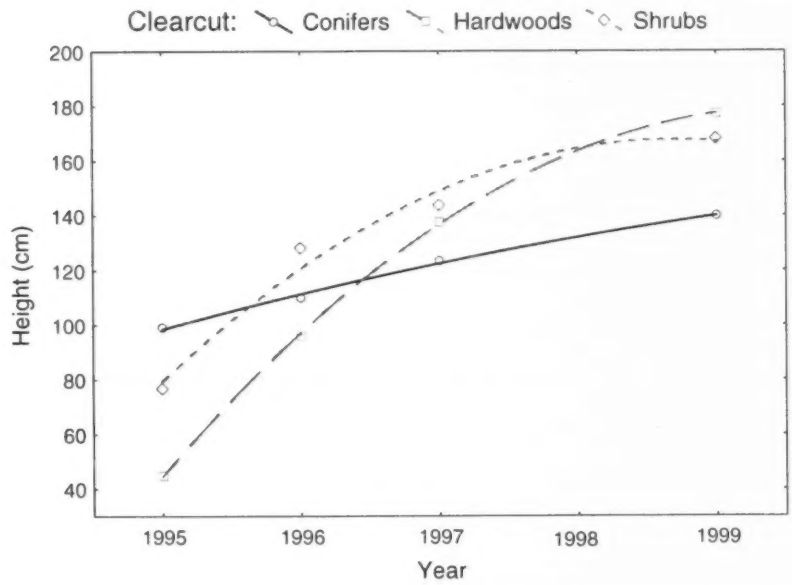

Fig. 6. Mean height trajectories of conifer advance regeneration, hardwood regeneration, and shrubs during the first 5 years after clearcutting.

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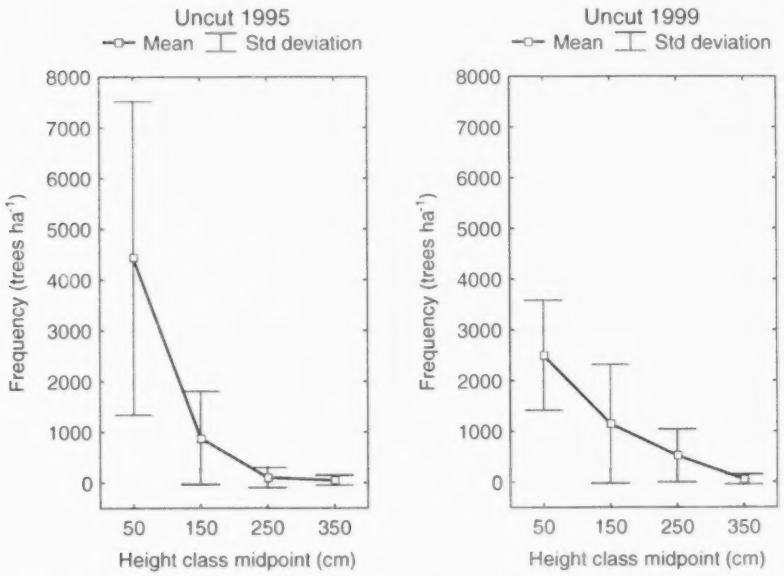

Fig. 7. Frequency distributions of conifer advance regeneration height in 1995 and 1999 for the uncut treatment.

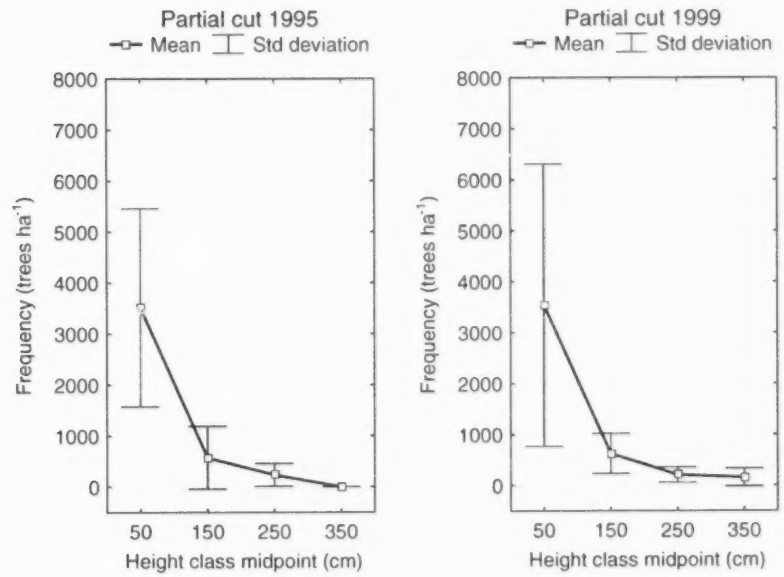

Fig. 8. Frequency distributions of conifer advance regeneration height in 1995 and 1999 for the partial cut treatment.

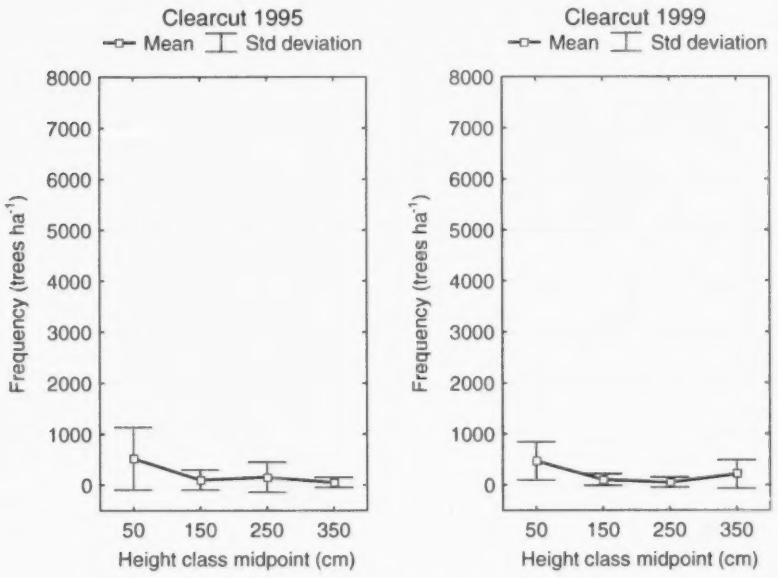

Fig. 9. Frequency distributions of conifer advance regeneration height in 1995 and 1999 for the clearcut treatment.

of light transmittance) that increases growth of conifer advance regeneration while limiting dominance by hardwood regeneration and non-crop competitors. The initially strong linear relationship between transmittance and BA reduction (Fig. 1) deteriorated as shade-intolerant shrubs and hardwood trees developed in the regeneration environment within 5 years of harvesting. Even during the first growing season after clearcutting, developing vegetation reduced understory PAR to half the above-canopy level. Since boreal plant community biomass peaks about 5 years after disturbance (Peltzer et al., 2000), rapidly declining light levels after harvesting restrict the window of opportunity for conifer regeneration development.

Favourable conditions for conifer growth may be obtained immediately after harvesting, but as light levels fall below required thresholds over the next few years, conifer advance regeneration may fail. Balsam fir and black spruce seedlings require full sunlight for optimum height growth (Logan, 1969). Similarly, annual height growth of white spruce saplings increases from 5 cm at 10% sunlight to 25 cm at 40% (Lieffers and Stadt, 1994).

4.2. Growth responses

Five years after harvesting, large variation in conifer height within each treatment (Table 3) likely resulted from initial differences in age, size, and vigour of conifer advance regeneration. White pine (*Pinus strobus* L.) advance regeneration has similar size variability under aspen canopies (Palik and Pregitzer, 1995). Hardwood height varied less (Table 4), reflecting the uniform characteristics of sucker-origin regeneration. In contrast to the conifer advance regeneration sampled in this study, growth patterns of planted conifers on BMW sites are more consistent than those of associated hardwood regeneration (MacDonald and Thompson, 2003).

Post-harvest height and abundance of hardwood regeneration and shrubs likely curtailed height response of conifer advance regeneration (Tables 3–5). Carbohydrate reserves in aspen parent root systems allow suckers to respond rapidly to canopy opening (Perala, 1990). In contrast, associated conifer advance regeneration, particularly low-vigour individuals, may delay responding to the sudden change in environmental conditions because of physiological shock

(Ruel et al., 2000). In northern Ontario aspen stands, air temperature extremes that could damage small conifer regeneration increase with canopy opening size (Carlson and Groot, 1997). Delayed conifer response is also evident in Québec, where balsam fir requires 6–10 years after harvesting to achieve maximum height growth (Doucet and Blais, 2000) and fir and spruce advance regeneration are rapidly dominated by competing non-crop species after clearcutting (Archambault et al., 1998).

The results of this study do not support using partial cutting to inhibit development of hardwoods and shrubs and promote conifer advance regeneration on BMW sites. For example, mean height of hardwood regeneration and shrubs exceeded that of conifer advance regeneration 5 years after partial cutting (Tables 3–5). Even with supplemental canopy thinning by forest tent caterpillar, the effect of the residual overstory may have combined with the effect of hardwoods and shrubs to reduce transmittance below the level required for competitive development of conifer advance regeneration. Advantages of over-story retention, such as microclimate moderation and competition reduction, are offset by reduced growth of conifer seedlings (Andersson, 1985) and advance regeneration (Kneeshaw et al., 1998). In western Canada, height growth of understory white spruce is maximized when light levels are above 40% and aspen BA is below 14 m^2 ha^{-1} (Comeau, 2001). Retaining only 25% of the overstory reduces light by 47% and limits height growth of shade-tolerant montane conifer seedlings (Mitchell, 2001).

To achieve full stocking of target species mixtures through natural regeneration, removing the entire overstory and controlling undesirable understory species before and after harvesting may be more reliable than partial cutting. Intensive management is often advisable to ensure adequate advance regeneration in mixed-species stands (Smith et al., 1997). For example, white spruce growth loss occurs with the first few competitors, and after 5 years seedling biomass under high competition is only about 10% of that under no competition (Jobidon, 2000). Vegetation control promotes growth of planted white spruce and jack pine (*Pinus banksiana* Lamb.) in partially cut and clearcut BMW stands in Ontario (Groot, 1999; MacDonald and Thompson, 2003) and may also be required to ensure that conifer advance regeneration develops into a vigorous understory component on harvested BMW sites. This consideration is particularly applicable to small advance regeneration, because height growth capacity is related to regeneration size (Lieffers et al., 1996; Orlander and Karlsson, 2000).

Maintaining dense canopies transmitting less than 10% light at the end of the rotation should eliminate persistent shrub and herb competitors prior to cutting, enhancing conditions for conifer regeneration (Lieffers et al., 1999). However, this approach may not be effective on BMW sites in Ontario, where competition is primarily post-cut vegetative reproduction of hardwood trees and shrubs.

Since balsam fir and black spruce are more shade-tolerant than white birch (*Betula papyrifera* Marsh.) and trembling aspen (Baker, 1949), maintaining a viable understory conifer component for the subsequent rotation may be more feasible than promoting conifer–hardwood overstories in the current rotation. Species mixtures perform best as vertical strata with shade-intolerant species in the overstory, and managing such stands relies on understanding the height growth dynamics of constituent species (Smith et al., 1997).

BA reduction level explained only 31% of conifer sapling DBH growth. However, conifer saplings benefited more than advance regeneration from overstory reduction because they were taller than 4 m when harvesting occurred, and most of their crown area was above the influence zone of rapidly expanding hardwood regeneration and shrubs. Similarly, small white pine seedlings are surpassed by hardwood regeneration after shelterwood cutting, but taller saplings remain competitive with the tallest hardwood regeneration (Kelty and Entcheva, 1993). In this study, the increase in sapling growth as BA was reduced implies that the entire hardwood overstory should be removed if adequate stocking of conifer saplings exists. However, some overstory retention may be advisable to protect conifer saplings from windthrow (Navratil et al., 1994). Furthermore, partially cutting BMW stands with well-distributed conifer saplings in the understory may foster codominant hardwood regeneration to create a blended species mixture suitable for removal 60–70 years later.

Partial cutting to release conifer saplings may not be appropriate on nutrient-poor sites, because understory conifers require sufficient nitrogen to utilize higher

light levels (Granhus and Braekke, 2001). This may be an important consideration on sites with aspen competition because suckers have access to carbohydrate reserves in the parent root system.

If the objective is to maximize growth of hardwood regeneration, harvesting should remove the entire overstory. Clearcutting promoted growth of both hardwood crop trees and shrubs (Figs. 3 and 4), but hardwoods remained dominant after 5 years (Tables 4 and 5). Canopy removal increases shrub development in Pennsylvania northern hardwood stands (Fredericksen et al., 1999) and coastal Oregon forests (Knowe et al., 1997), but favours growth of hardwood regeneration in mixedwood stands in Manitoba (Ball and Walker, 1995) and Québec (Prevost and Pothier, 2003) and central hardwood stands in the United States (Dale et al., 1995).

Adjusting the harvest season may influence which BMW species regenerate successfully. For example, litter disturbance associated with summer logging or scarification exposes aspen roots to higher temperatures and may stimulate sucker production (Lavertu et al., 1994). However, harvesting in the dormant season, when carbohydrate levels in roots are highest, also promotes suckering (Perala, 1990). In this study, winter logging resulted in sufficient aspen competition to restrict height growth of conifer advance regeneration (Tables 3 and 4).

Harvest intensity should be adapted to overstory species composition. In aspen-spruce stands in Alberta, hardwood-dominated overstories transmit 14–40% light, while conifer canopies transmit only 5–11% (Lieffers and Stadt, 1994). Similarly, in boreal Québec stands, light levels are higher under shade-intolerant species of *Populus*, *Betula*, and *Pinus* than under shade-tolerant conifers (Messier et al., 1998). Thus, in conifer-dominated stands heavier cutting is required to promote growth of conifer advance regeneration, assuming hardwood competitors are controlled.

4.3. Height trajectories

The large height variation in all species groups (Tables 3–5) prevents detailed interpretation of height trajectories (Figs. 5 and 6). Since the differences in curve shape and position among species groups may arise partly from uncontrolled variation in mean heights, the trajectories can be used for summarizing observations and generating hypotheses, but not for inferring responses in a broader population. They reveal the difficulty in distinguishing developmental trends and relative dominance among species groups during the first few years after treatment.

The relative performance of associated crop species following different harvesting strategies should be monitored long enough to determine whether mid-rotation interventions are necessary to achieve stand structure objectives. For example, the relative position of conifer advance regeneration may decline as hardwoods and shrubs progressively increase their dominance in partial cuts and clearcuts (Figs. 5 and 6). Similar post-cut dynamics involving conifer regeneration and competitors have been reported elsewhere (Lautenschlager, 1995; Archambault et al., 1998). Potential overtopping of conifer advance regeneration following canopy opening on mixedwood sites emphasizes the importance of considering selective vegetation management to maintain the conifer component.

Hardwood crop tree regeneration should also be monitored for many years after harvesting, particularly if any overstory is retained. For example, 5 years after partial cutting, mean height of hardwoods was less than that of shrubs (Fig. 5).

Mean height of regeneration and shrubs may have levelled off earlier in the partial cut treatment than in the clearcut treatment because residuals refoliated after a brief forest tent caterpillar defoliation. Even without this refoliation effect, residual crown expansion following partial cutting compounds the effect of understory competition on growth of crop tree regeneration. Complex vegetation dynamics following partial cutting in mixedwood stands (Smidt and Puettmann, 1998) necessitate long-term monitoring and possibly stand interventions to attain desired species compositions and stand structures.

The large reduction in mean density and increase in mean height of conifer advance regeneration 1 year after clearcutting (Table 6) imply mortality in small size classes. This effect would explain the difference in mean height of conifer advance regeneration between partially cut and clearcut plots (Table 3; Figs. 5 and 6). During clearcutting, the feller-buncher frequently had to move through regeneration to allow the cutting head to reach trees far from equipment trails.

Table 6
Height and density of conifer advance regeneration[a] before treatment (1994) and after treatment (1995)

Treatment	Height (cm)				Density (stems ha^{-1})			
	1994		1995		1994		1995	
	Mean	S.D.[b]	Mean	S.D.	Mean	S.D.	Mean	S.D.
Uncut	60.85	45.25	56.92	58.20	4896	4398	5469	5409
Partial cut	49.37	40.07	56.92	59.30	4063	4981	4323	4293
Clearcut	57.85	52.14	98.99	114.70	2083	2755	833	1925

[a] Trees <4.0 m tall.
[b] Standard deviation.

During partial cutting, such trees could be left as residuals, reducing equipment movement and associated regeneration damage. Density reductions caused by logging damage are reported elsewhere; for example, mortality of Norway spruce (*Picea abies* [L.] Karst.) advance regeneration increases with cutting intensity (Granhus and Fjeld, 2001) and is highest in small size classes (Orlander and Karlsson, 2000).

4.4. Conifer height distributions

The large height variation typical of conifer advance regeneration (Palik and Pregitzer, 1995) was confirmed in this study (Figs. 7–9). Despite this variation, height distribution trends with implications for mixedwood management emerged. In the partial cut and clearcut treatments, density shifts over 4 years into larger height classes were inadequate to develop a codominant conifer component in the next rotation. Lower densities of small trees in the clearcut 1 and 5 years after harvesting may be explained by lower initial densities (Table 6) and more potentially damaging machine activity. First-year (1995) seedling densities in the 50 cm class were likely inadequate even in the uncut and partial cut treatments (approximately 4400 and 3500 trees ha^{-1}, respectively), considering the high attrition rate between the 50 and 150 cm classes.

Evidence from other studies indicates that high initial densities are required to maintain conifers in mixedwood stands. For example, Greene et al. (2002) found that a minimum of 26,000 trees ha^{-1} of balsam fir advance regeneration is required in eastern Canada to achieve full stocking. Since potential damage during harvesting (Granhus and Fjeld, 2001) limits the role of advance regeneration, artificial or assisted natural regeneration of conifers should be prescribed where necessary. Supplementary regeneration efforts may be required to obtain uniform stocking of desired species because of the variability inherent in BMW stands (Table 1). Although balsam fir natural regeneration may become established on unprepared ground, white spruce requires microsites with minimal litter and humus cover (Nienstaedt and Zasada, 1990; Prevost and Pothier, 2003). Techniques such as scarifying large patches, retaining fallen logs, and establishing raised mounds are effective for promoting spruce establishment under trembling aspen (DeLong et al., 1997).

5. Conclusion

Partial cutting to release advance regeneration cannot be recommended as an alternative to herbicides for maintaining conifers in BMW stands, because height growth of hardwood trees and shrubs exceeded that of conifers in partially cut plots. In western Canadian BMW stands, leaving a residual overstory suppresses hardwood regeneration and favours associated conifers (Waldron and Kolabinski, 1994; Man and Lieffers, 1999). However, this approach may not be as effective in eastern Canadian BMW stands, because of different climatic conditions and vegetation dynamics. Shading by residual trees generally reduces aspen suckering (Perala, 1977), but in this study, suckering after partial cutting was adequate to suppress growth of associated conifer advance regeneration.

Partial cutting may not be economically feasible because initial harvest volumes are low and access roads require maintenance to allow future residual removal. Furthermore, relying on conifer advance

regeneration reduces control over conifer species composition in the next rotation. In northern Ontario BMW stands, balsam fir is often the predominant species of natural regeneration (Yang and Fry, 1981; Arnup, 1996), but forest companies prefer spruce (MacDonald and Cormier, 1998). Since companies may be slow to accept unfamiliar species (Smith et al., 1997), partial cutting to release advance regeneration requires reliable information on the pre-cut stocking of desirable conifer species in the understory.

In this study, conifer sapling growth responded moderately to BA reduction, indicating that partial cutting may help meet silvicultural objectives in mixedwood stands that are well-stocked with tall saplings. Partial cutting may also be prescribed to enhance resource values unrelated to regeneration success or volume yield, such as plant diversity and structural complexity (Tappeiner and Hennon, 2002), recruitment of snags and coarse woody debris (Lee et al., 1997), and bird abundance (Norton and Hannon, 1997).

The indication that long-term monitoring is needed to evaluate the relative dominance of associated species following different harvest intensities confirms the results of other studies. For example, eight growing seasons are required to assess growth advantages in black spruce regeneration after vegetation control on BMW sites (Fleming et al., 1996), and 10th-year height increments may be inadequate for predicting the relative position of upland boreal conifers 25 years after harvesting (Doucet and Blais, 2000).

The presence of large growth variation emphasizes the need for extensive sampling across a variety of BMW ecosites to confirm the responses of conifer and hardwood regeneration and shrubs to varying levels of BA reduction. Since balsam fir was the main conifer species in this study, responses of white and black spruce advance regeneration should be investigated in future studies. The effects of other factors, such as season of harvest, degree of soil disturbance, and pattern of overstory removal, should also be considered.

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References

Andersson, S.-O., 1985. Treatment of young mixed stands with birch and conifers. In: Hägglund, B., Peterson, G. (Eds.), Broadleaves in Boreal Silviculture—An Obstacle or an Asset? Report No. 14. Swedish University of Agricultural Sciences, Department of Silviculture, Umea, Sweden, pp. 127–161.

Archambault, L., Morissette, J., Bernier-Cardou, M., 1998. Forest succession over a 20-year period following clearcutting in balsam fir–yellow birch ecosystems of eastern Quebec, Canada. For. Ecol. Manage. 102, 61–74.

Arnup, R.W., 1996. Stand and site conditions associated with the abundance and distribution of black spruce and balsam fir advance growth in northeastern Ontario. NODA-NFP Technical Report No. TR-29. Can. For. Serv., Sault Ste. Marie, ON, 38 pp.

Baker, F.S., 1949. A revised tolerance table. J. For. 47, 179–181.

Ball, W.J., Walker, N.R., 1995. Natural regeneration of white spruce after partial cutting and strip scarification in mature mixed white spruce-aspen stands, Manitoba. Can. For. Serv., Winnipeg, MB, 46 pp.

Bergeron, Y., Harvey, B., 1997. Basing silviculture on natural ecosystem dynamics: an approach applied to the southern boreal mixedwood forest of Quebec. For. Ecol. Manage. 92, 235–242.

Carlson, D.W., Groot, A., 1997. Microclimate of clear-cut, forest interior, and small openings in trembling aspen forest. Agric. For. Meteorol. 87, 313–329.

Comeau, P.G., 2001. Relationships between stand parameters and understorey light in boreal aspen stands. B.C. J. Ecosyst. Manage. 1, 1–8.

Dale, M.E., Smith, H.C., Pearcy, J.N., 1995. Size of clearcut opening affects species composition, growth rate, and stand characteristics. Research Paper No. NE-698. USDA For. Serv., Northeastern For. Exp. Sta., Radnor, PA, 21 pp.

DeLong, H.B., Lieffers, V.J., Blenis, P.V., 1997. Microsite effects on first-year establishment and overwinter survival of white spruce in aspen-dominated boreal mixedwoods. Can. J. For. Res. 27, 1452–1457.

Doucet, R., Blais, L., 2000. Comparative growth of balsam fir and black spruce advance regeneration after logging. J. Sust. For. 10, 235–239.

Fleming, R.A., Wood, J.E., Griffith, J.A., 1996. Modelling the effects of herbicide release on early growth and survival of *Picea mariana*. N. Z. J. For. Sci. 26, 202–221.

Fraser, E.C., Lieffers, V.J., Landhausser, S.M., Frey, B.R., 2002. Soil nutrition and temperature as drivers of root suckering in trembling aspen. Can. J. For. Res. 32, 1685–1691.

Fredericksen, T.S., Ross, B.D., Hoffman, W., Morrison, M.L., Beyea, J., Johnson, B.N., Lester, M.B., Ross, E., 1999. Short-term understory plant community responses to timber-harvesting intensity on non-industrial private forestlands in Pennsylvania. For. Ecol. Manage. 116, 129–139.

Granhus, A., Braekke, F.H., 2001. Nutrient status of Norway spruce stands subjected to different levels of overstorey removal. Trees 15, 393–402.

Granhus, A., Fjeld, D., 2001. Spatial distribution of injuries to Norway spruce advance growth after selection harvesting. Can. J. For. Res. 31, 1903–1913.

Greene, D.F., Kneeshaw, D.D., Messier, C., Lieffers, V., Cormier, D., Doucet, R., Coates, K.D., Groot, A., Grover, G., Calogeropoulos, C., 2002. Modelling silvicultural alternatives for conifer regeneration in boreal mixedwood stands (aspen/white spruce/balsam fir). For. Chron. 78, 281–295.

Groot, A., 1999. Effects of shelter and competition on the early growth of planted white spruce (*Picea glauca*). Can. J. For. Res. 29, 1002–1014.

Hearnden, K.W., Millson, S.V., Wilson, W.C., 1992. A Report on the Status of Forest Regeneration. Ont. Min. Nat. Resour., Indep. Forest Audit Committee, Toronto, ON, 117 pp.

Jobidon, R., 2000. Density-dependent effects of northern hardwood competition on selected environmental resources and young white spruce (*Picea glauca*) plantation growth, mineral nutrition, and stand structural development—a 5-year study. For. Ecol. Manage. 130, 77–97.

Kelty, M.J., Entcheva, P.K., 1993. Response of suppressed white pine saplings to release during shelterwood cutting. N. J. Appl. For. 10, 166–169.

Kneeshaw, D., Bergeron, Y., de Grandpre, L., 1998. Early response of *Abies balsamea* seedlings to artificially created openings. J. Veg. Sci. 9, 543–550.

Knowe, S.A., Stein, W.I., Shainsky, L.J., 1997. Predicting growth response of shrubs to clear-cutting and site preparation in coastal Oregon forests. Can. J. For. Res. 27, 217–226.

Lautenschlager, R.A., 1995. Competition between forest brush and planted white spruce in North-Central Maine. N. J. Appl. For. 12, 163–167.

Lautenschlager, R.A., Bell, F.W., Wagner, R.G., Reynolds, P.E., 1998. The Fallingsnow ecosystem project: documenting the consequences of conifer release alternatives. J. For. 96, 20–27.

Laverty, D., Mauffette, Y., Bergeron, Y., 1994. Effects of stand age and litter removal on the regeneration of *Populus tremuloides*. J. Veg. Sci. 5, 561–568.

Lee, P.C., Crites, S., Nietfeld, M., Nguyen, H.V., Stelfox, J.B., 1997. Characteristics and origins of deadwood material in aspen-dominated boreal forests. Ecol. Appl. 7, 691–701.

Lieffers, V.J., Stadt, K.J., 1994. Growth of understory *Picea glauca*, *Calamagrostis canadensis*, and *Epilobium angustifolium* in relation to overstory light transmission. Can. J. For. Res. 24, 1193–1198.

Lieffers, V.J., Stadt, K.J., Navratil, S., 1996. Age structure and growth of understory white spruce under aspen. Can. J. For. Res. 26, 1002–1007.

Lieffers, V.J., Messier, C., Stadt, K.J., Gendron, F., Comeau, P.G., 1999. Predicting and managing light in the understory of boreal forests. Can. J. For. Res. 29, 796–811.

Logan, K.T., 1969. Growth of tree seedlings as affected by light intensity. IV. Black spruce, white spruce, balsam fir, and eastern white cedar. Publication No. 1256. Can. For. Serv., Ottawa, ON, 12 pp.

MacDonald, G.B., 1995. The case for boreal mixedwood management: an Ontario perspective. For. Chron. 71, 725–734.

MacDonald, G.B., Cormier, R.G., 1998. Commercial utilization of the boreal mixedwood forest. Sci. Tech. Ser., vol. 9. Boreal Mixedwood Notes No. 21. Ont. Min. Nat. Resour., Terr. Ecosys. Br., Sault Ste. Marie, ON, 7 pp.

MacDonald, G.B., Thompson, D.J., 2003. Responses of planted conifers and natural hardwood regeneration to harvesting, scalping, and weeding on a boreal mixedwood site. For. Ecol. Manage. 182, 213–230.

Man, R., Lieffers, V.J., 1999. Effects of shelterwood and site preparation on microclimate and establishment of white spruce seedlings in a boreal mixedwood forest. For. Chron. 75, 837–844.

Messier, C., Parent, S., Bergeron, Y., 1998. Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. J. Veg. Sci. 9, 511–520.

Mitchell, A.K., 2001. Growth limitations for conifer regeneration under alternative silvicultural systems in a coastal montane forest in British Columbia, Canada. For. Ecol. Manage. 145, 129–136.

Navratil, S., Brace, L.G., Sauder, E.A., Lux, S., 1994. Silvicultural and harvesting options to favor immature white spruce and aspen regeneration in boreal mixedwoods. Inf. Rep. No. NOR-X-337. Can. For. Serv., Edmonton, AB, 78 pp.

Newmaster, S.G., Bell, F.W., Vitt, D.H., 1999. The effects of glyphosate and triclopyr on common bryophytes and lichens in northwestern Ontario. Can. J. For. Res. 29, 1101–1111.

Nienstaedt, H., Zasada, J.C., 1990. White spruce. In: Burns, R.M., Honkala, B.H. (Eds.), Silvics of North America, vol. 1. Conifers. USDA For. Serv. Agric. Handb. 654, pp. 204–226.

Norton, M.R., Hannon, S.J., 1997. Songbird response to partial-cut logging in the boreal mixedwood forest of Alberta. Can. J. For. Res. 27, 44–53.

Orlander, G., Karlsson, C., 2000. Influence of shelterwood density on survival and height increment of *Picea abies* advance growth. Scand. J. For. Res. 15, 20–29.

Palik, B.J., Pregitzer, K.S., 1995. Height growth of advance regeneration under an even-aged bigtooth aspen (*Populus grandidentata*) overstory. Am. Midl. Nat. 134, 166–175.

Peltzer, D.A., Bast, M.L., Wilson, S.D., Gerry, A.K., 2000. Plant diversity and tree responses following contrasting disturbances in boreal forest. For. Ecol. Manage. 127, 191–203.

Perala, D.A., 1977. Manager's handbook for aspen in the north-central states. Gen. Tech. Rep. NC-36. USDA For. Serv., North Central For. Exp. Sta., St. Paul, MN, 36 pp.

Perala, D.A., 1990. Quaking aspen. In: Burns, R.M., Honkala, B.H. (Eds.), Silvics of North America, vol. 2. Hardwoods. USDA For. Serv. Agric. Handb. 654, pp. 555–569.

Prevost, M., Pothier, D., 2003. Partial cuts in a trembling aspen—conifer stand: effects on microenvironmental conditions and regeneration dynamics. Can. J. For. Res. 33, 1–15.

Ruel, J.C., Messier, C., Doucet, R., Claveau, Y., Comeau, P., 2000. Morphological indicators of growth response of coniferous advance regeneration to overstorey removal in the boreal forest. For. Chron. 76, 633–642.

Smidt, M.F., Puettmann, K.J., 1998. Overstory and understory competition affect underplanted eastern white pine. For. Ecol. Manage. 105, 137–150.

Smith, D.M., Larson, B.C., Kelty, M.J., Ashton, P.M.S., 1997. The Practice of Silviculture: Applied Forest Ecology, 9th ed. Wiley, New York, 537 pp.

Tappeiner, J.C., Hennon, P.E., 2002. Developing silvicultural systems based on partial cutting in western hemlock-Sitka spruce stands of southeast Alaska. Forestry 75, 425–431.

Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T., Lehman, C., 2001. Diversity and productivity in a long-term grassland experiment. Science 294, 843–845.

Waldron, R.M., Kolabinski, V.S., 1994. Uniform shelterwood cutting and scarifying in white spruce-trembling aspen stands to induce natural white spruce regeneration, Manitoba and Saskatchewan. Can. For. Serv., Winnipeg, MB, 53 pp.

Yang, R.C., Fry, R.D., 1981. Natural succession following harvesting in the boreal mixedwood forest. In: Whitney, R.D., McClain, K.M. (Cochairmen), Boreal Mixedwood Symposium. COJFRC Symp. Proc. O-P-9. Min. Supply and Serv. Can., Ottawa, ON, pp. 65–77.

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